

Article Addendum

A male's playback signal turns female *Marcusenius pongolensis* receivers on or off depending on his behavioural state

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The electric organ discharges (EODs) of male southern bulldog fish, *Marcusenius pongolensis*, are of longer pulse duration than those of females, and grow with body size.¹ In a playback experiment, male EODs of longer pulse duration were more attractive to females in terms of association time and other behavioural variables.² Here, we show that the greater attraction of long male EODs to females was only revealed when combined with 'acceptable' information on his behavioural state (the combination was manipulated experimentally). Females were attracted to long EODs had the male (apparently) been in a nocturnally-active but non-aggressive behavioural state, but the preference vanished when in a diurnally 'resting' or nocturnal aggression (agonistic) state. Information on male behavioural state was conveyed to females by one of four types of inter-discharge interval (IDI) pattern that were used to drive the presentation of EODs.

Weakly electric pulse fish generate electric organ discharges (EODs) for nocturnal electrocommunication and electrolocation.³⁻⁷ In mormyrid fish, the individual EOD pulse waveform usually is stable over extended periods of time.⁸⁻¹⁰ The EOD waveform may convey information as to species, sex and individual identity. Even though EOD waveform is species-specific, it may differ significantly amongst individuals; for example, in pulse duration between the sexes.^{4,8-12} In mormyrid fish of the genus *Pollimyrus*, conditioned and unconditioned discrimination tests have demonstrated sensory discrimination of minute individual waveform differences on the microsecond scale.¹³⁻¹⁵ In contrast to *Marcusenius pongolensis* females, the males' EOD pulse duration increases with standard length over lifetime from maturity onward.¹ An *M. pongolensis* male's playback EOD of longer pulse duration evoked stronger aggressive responses from a territory holder.¹⁶ A territorial male's EOD pulse duration,

and rate of aggressive behaviour, increased when his familiar neighbour, separated by plastic mesh in their common tank, was replaced by a stranger male. EOD pulse duration receded again when sensory contact was severely restricted by the introduction of a tightly fitting, solid plastic wall.¹⁷ These results suggest that in evolution the long EOD pulse duration in the male *M. pongolensis* has been shaped by male competition.

We studied the possibility of female mate choice shaping male pulse duration in addition to male competition in *M. pongolensis*, using playback experiments that excluded all sensory modalities except the electrical. Following an unforced alternative choice paradigm, we simultaneously played back two different male EOD waveforms via two electric fish decoys, positioned symmetrically to a female's right and left. We recorded a female's responses as association time with stimulators, and as attack rates. For playback we had first to choose an inter-discharge interval (IDI) pattern to drive the presentation of EOD pulses. Associated with diurnal hiding behaviour ('rest'), nocturnal swimming activity, either locomotory or when foraging, and territorial aggression, IDI patterns differ widely in mormyrids.^{3,4,7,18} For example, IDIs generated by males during agonistic behaviour are characterised by rapid transitions from high to low discharge rates and vice versa, and long discharge breaks. On the other hand, IDIs generated by foraging individuals are characterised by rather constant, medium discharge rates. Figure 1 shows IDI patterns recorded from male *M. pongolensis* in four different behavioural states (agonistic, resting, foraging and exploratory behaviour). We defined 'foraging' as nocturnal locomotion in the presence of food, and 'exploratory behaviour' as nocturnal locomotion in the absence of food. We examined the suitability of each of these four types of IDI pattern for testing female mate choice in a playback experiment preceding the main tests (that were reported in Machnik and Kramer 2008; where further experimental detail may be found).² We used two IDI patterns per pattern type, recorded from two different male *M. pongolensis* individuals (Werneyer and Kramer (2002);¹⁸ Table 1, present study). We used six EODs (of 320 to 716 μ s pulse duration, recorded in the field) from six different male *M. pongolensis*, and we presented every EOD with each IDI just once. We observed strongest female preference for long pulses with the 'foraging' and the 'exploratory' IDI patterns in four out of five experimental subjects. Subject E4, which did not show any preferences, later developed physical abnormalities and may have been unhealthy already at this

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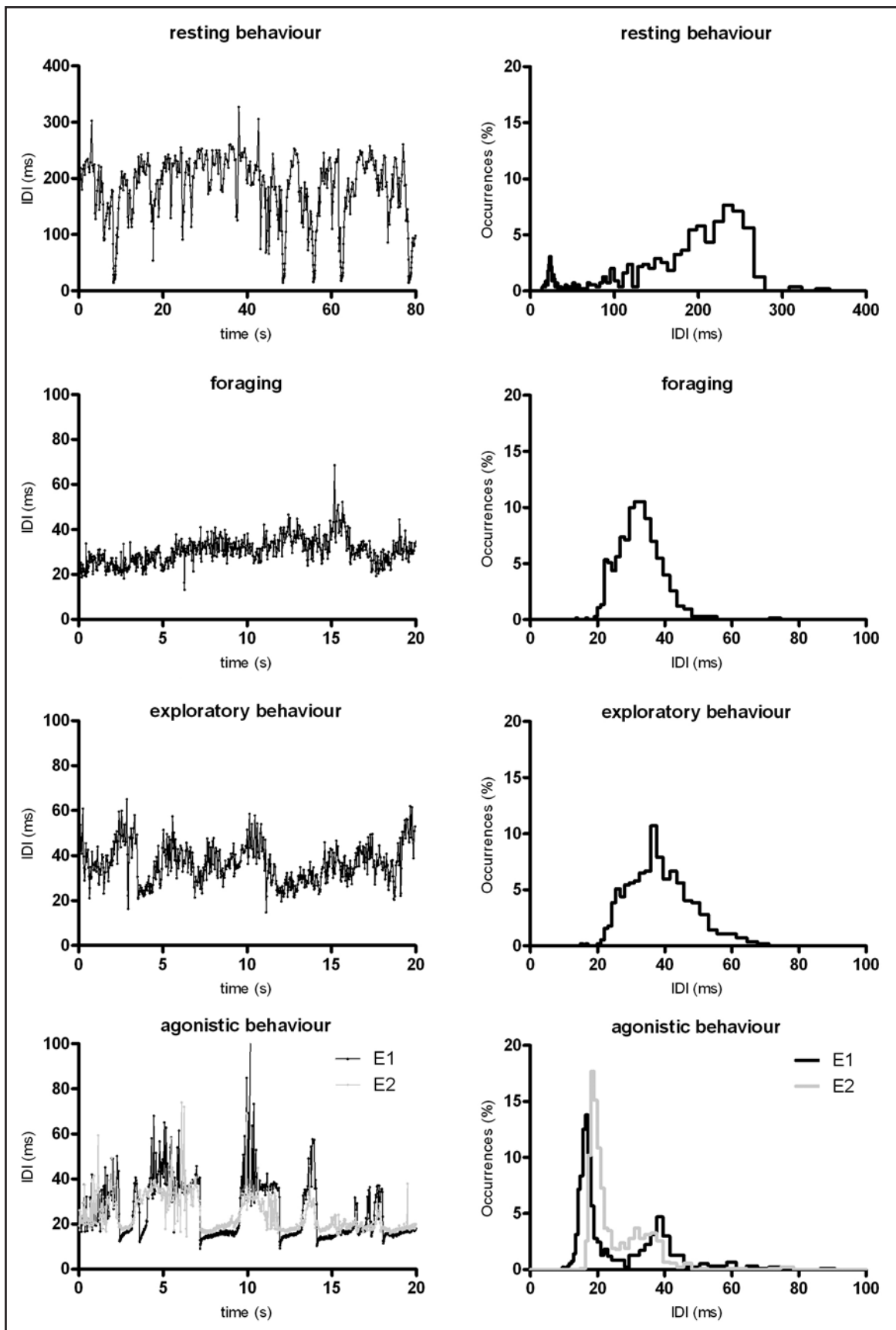


Figure 1. Examples of inter-discharge interval (IDI) patterns for four behavioural states (resting, foraging, exploratory and agonistic behaviours). *Left*, *ordinates* give duration of individual IDIs [ms], *abscissas* time [s]. Each point is one interval; points are connected by lines to show trend. Histograms on the right represent data to their left. *Lowest*, EOD activity for agonistic behaviour between males E1 and E2, and associated IDI patterns and histograms.

Table 1 Descriptive statistics for the inter-discharge interval patterns used for playback

IDI pattern	Total duration (s)	I_{\min} (ms)	I_{mean} (ms)	I_{\max} (ms)	Mean EOD rate (Hz)	# Intervals (N)
Agonistic #1	30	18.45	38.27	76.49	26.17	785
Agonistic #2	30	27.47	45.65	100.34	21.93	658
Exploratory #1	30	23.90	28.86	38.00	34.63	1039
Exploratory #2	30	23.48	29.22	38.10	34.20	1026
Foraging #1	30	21.87	31.22	50.30	31.93	958
Foraging #2	30	25.00	30.20	59.41	33.10	993
Resting #1	30	61.71	254.13	342.34	3.93	118
Resting #2	30	57.41	245.36	501.06	4.07	122

I_{\min} , I_{\max} , shortest and longest interval in IDI pattern; I_{mean} , mean interval; # Intervals: total number of intervals in IDI pattern.

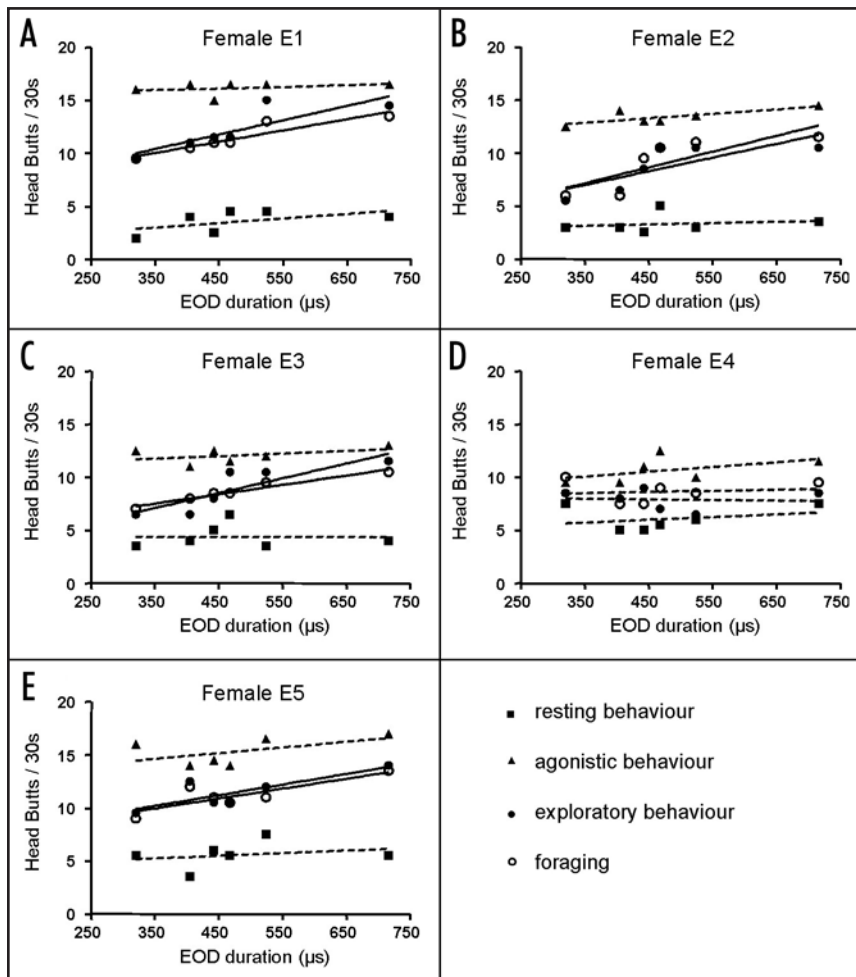


Figure 2. The dependency of the rate of head butts (ordinates), as evoked by playback, on playback pulse duration (abscissas, in μs). Each point is the average of two repeats. Least-squares regression line significantly ($p \leq 0.05$) different from slope zero except where shown as a broken line. All experimental females except E4 responded more strongly to the playback of long male EODs when combined with foraging or exploratory IDI pattern.

time. When using 'agonistic' or 'resting' IDI patterns, the correlation between the experimental females' choice behaviour and stimulus pulse duration vanished in all females (Fig. 2, Table 2).

The most effective IDI patterns, foraging and exploratory, were highest in mean discharge rate (Table 1), and this fact alone

could account for greater excitation (arousal) in the experimental subjects as compared to the other IDI patterns. However, the 'agonistic' patterns evoked the strongest, albeit indiscriminate, responses from experimental subjects despite its lower mean discharge rate (but including many rapid transitions between extremely low and high discharge rates not observed in the 'exploratory' and 'foraging' patterns). The playback of 'agonistic' patterns seemed to represent a threat to the experimental subjects, such as potential competition for hiding places, territory or food, and evoked full-fledged attack behaviour aimed at the fish decoys when discrimination amongst the individual characteristics of the 'intruder' EODs had, apparently, become irrelevant. By contrast, the playback of 'resting' IDI patterns with their low mean discharge rates evoked generally weaker responses and aggression (see number of head butts aimed at the active dipole). There was a trend for female preference of long EODs when presented with a 'resting' IDI pattern (not significant). However, 'foraging' and 'exploratory' patterns were much more effective in evoking female choice behaviour according to EOD pulse duration, and were therefore adopted for the main tests (that confirmed female mate choice, the preference of male EOD pulses of long duration; as reported in Machnik and Kramer 2008).²

What is it that makes 'foraging' and 'exploratory' patterns the most suitable ones for the present application among the four pattern types tested? Apparently, it is their lack of extreme discharge rate values and lack of rapid transitions from low to high rates and vice versa, compared to the other patterns. Even in the 'resting' pattern, despite its mean discharge rate being lowest, there were instantaneous high discharge rates, even though these periods were very short and relatively infrequent. By their relative constancy in discharge rate and their lack of extremes, 'foraging' and 'exploratory' patterns resembled 'spawning' IDI patterns, although these were of still lower discharge rate and maintained only for the short duration of an individual spawning bout in these fractional spawners (a few seconds).¹⁹ 'Spawning' IDI patterns might therefore be still

better suited than the 'foraging' and 'exploratory' patterns we used; however, their short duration per bout, separated by other EOD activity until the next spawning bout occurred, made them less suitable for a playback experiment of a certain minimum duration.

The choice of a suitable IDI pattern for playback experiments with *M. pongolensis* has been determined as critical for success in the present study. With an uninformed choice we might have failed to observe female mate choice entirely, and the suggestion that sexual selection by females has very likely shaped the male EOD pulse duration in *M. pongolensis* (Machnik and Kramer 2008)² would have no experimental support.

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Table 2 **Linear regression for the dependency of the rate of head butts on stimulus EOD pulse duration for different IDI patterns**

IDI pattern	Slope \pm sem	y-intercept \pm sem	r ²	F	p
Resting	0.004 \pm 0.005	1.5 \pm 2.3	0.0823	0.8967	0.3660
Agonistic	0.001 \pm 0.003	15.5 \pm 1.3	0.0293	0.3016	0.5949
Exploratory	0.014 \pm 0.003	5.7 \pm 1.6	0.6399	17.77	0.0018
Foraging	0.011 \pm 0.002	6.3 \pm 1.2	0.6559	19.06	0.0014

sem: standard error of mean; p: level of significance ($\alpha \leq 0.05$), d.f. = 1,10. Example given is for experimental female E1; three other individuals with similar results, plus one with non-significant results on all IDI patterns.